SECONDARY CHANGES IN MICRO-ORNAMENTATION OF SOME DEVONIAN AMBOCOELIID BRACHIOPODS

by ANDRZEJ BALIŃSKI

ABSTRACT. Studies on some species of the Ambocoeliidae from the Devonian of Poland have shown that their micro-ornamentation may be completely changed by secondary factors such as weathering, which leads to the separation of initially invisible coarse-crystalline structures, known as microspines, from the primary shell layer. Thus, secondary microspinosity appears on the surface of originally smooth or radially ornamented specimens. The recognition of primary and secondary micro-ornamentation is shown to be important in taxonomic studies. Comparative studies show that the microspines in the Ambocoeliidae are probably homologous to the microspines *sensu stricto* in other representatives of the Spiriferida.

ON the basis of data drawn from the literature, representatives of the Ambocoeliidae may be divided in regard to micro-ornamentation into forms with (*a*) radial ornamentation, (*b*) microspines, and (*c*) quite smooth. All three types of micro-ornamentation are considered as primary and considerable specific and generic taxonomic importance is ascribed to them.

As shown by observations on some ambocoeliid species from the Devonian of Poland, e.g. *Ambothyris infima* (Whidborne), *Crurithyris inflata* (Schnur), *C. jurkowicensis* Baliński, and *Ilmenia hians* (Buch), the character of the micro-ornamentation may be completely changed by secondary factors (e.g. weathering) even in a single specimen. The progressive process of weathering leads to a gradual separation, from the primary shell layer, of originally invisible, coarse-crystalline structures called microspines, which form a characteristic micro-ornamentation on the surface of weathered specimens known as microspinosity. Complying with the accepted taxonomic principles, one could, therefore, assign the weathered (with microspines) and unweathered (with the primary micro-ornamentation preserved in the form of capillae, or quite smooth) specimens of the same species to different genera.

Since the problem of the microspines in the ambocoeliids has not so far been explained conclusively, the term microspines, as applied to the ambocoeliids, will be used herein in quotation-marks ('microspines'), so as to distinguish them from the true microspines, which occur in other forms, e.g. *Nucleospira lens* (Schnur) or *Reticulariina spinosa* (Norwood and Pratten).

Material and techniques

A major part of this study was based on the specimens of the following four Middle Devonian (Givetian) species from the Holy Cross Mountains, Poland: *Ambothyris infima* (Whidborne), *Crurithyris jurkowicensis* Baliński and *Ilmenia hians* (Buch) from the Jurkowice-Budy (Baliński 1973), and *Crurithyris inflata* (Schnur) from the Skały (Biernat 1966). Specimens of *Nucleospira lens* (Schnur) and *Proreticularia dorsoplana* Gürich from the Middle Devonian of Swietomarz-Sniadka, Holy Cross Mountains (Gürich 1896), were used for comparative studies.

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All specimens studied were obtained from the shales or weathered marly limestones by washing and studied with a JSM-2 scanning electron microscope. All specimens were cleaned ultrasonically and coated in two stages with carbon and gold.

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Ilmenia hians (Buch)

A distinct micro-ornamentation in the form of radial capillae covering the entire shell from beak to the anterior margin (Pl. 32, figs. 1 (bottom part of the figure), 4; text-fig. 1A) is visible on the specimens with a well-preserved primary shell layer. These capillae (five–nine per mm) are limited to the primary shell layer though a few specimens show slight indication of them on the secondary shell layer (Pl. 32, fig. 1 (top part of the figure)).

Specimens from scree or a porous rock are generally etched to a varying degree as a result of the action of water containing various acid residues (e.g. HCO_3^-, humic acids, etc.), and progressive weathering sometimes leads to a complete change in primary micro-ornamentation. In the first stage the characteristic, elongate corrosion pits, which on enlargement reveal a fibrous secondary shell layer, appear on the ridges of capillae (Pl. 32, fig. 1 (bottom part of the figure); text-fig. 1B). Further weathering causes a corrosion of capillae over their entire length as deep as the secondary shell layer. Only the streaks of the primary shell layer, which form furrows between capillae in the uncorroded part, remain intact. Thus, a complete inversion of the primary micro-ornamentation occurs and the primary prominent elements (capillae) become replaced by grooves and vice versa, the ridges formed of the primary shell layer correspond to the primary grooves between capillae (Pl. 32, fig. 1 (central part of the figure); Pl. 33, fig. 1; text-fig. 1C).

The resistance to solution of the primary shell layer in intercapillary grooves should be ascribed to the coarsely crystalline structures arranged in precise radial rows between capillae. With progressive weathering the coarsely crystalline structures separate more and more from the primary shell layer, forming a characteristic micro-ornamentation described in some ambocoeliids as a microspinosity (Pl. 32, fig. 5). Thus, a single specimen may have two completely different types of micro-ornamentation, namely, capillae (primary) and 'microspines' (secondary) (Pl. 32, fig. 1 (the lower- and uppermost parts of the figure)). The character of 'microspinosity' in *Ilmenia hians* (Buch) is particularly like that in *Ilmenispina hanaica* Havlíček

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EXPLANATION OF PLATE 32

Fig. 1. Scanning electron micrograph. Consecutive stages of changes in micro-ornamentation on the brachial valve of *Ilmenia hians* (Buch), umbonal part at the top of figure (see also fig. 4), ×50.

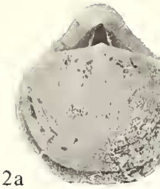
Fig. 2. Dorsal and lateral views of shell of *Proreticularia dorsoplana* Gürich, ×4.

Fig. 3. Dorsal and lateral views of shell of *Nucleospira lens* (Schnur), ×4.

Figs. 4, 5. Two brachial valves of *I. hians* (Buch). 4, showing primary. 5, showing secondary micro-ornamentation; ×7, ×6 respectively.

Abbreviations on all plates: C—trace of central canal; G—intercapillary grooves; PL—primary shell layer; R—ridges of capillae; S—'microspines'; SL—secondary shell layer.

1



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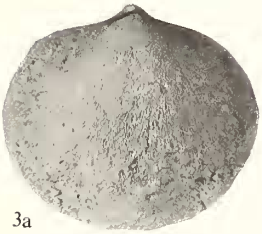

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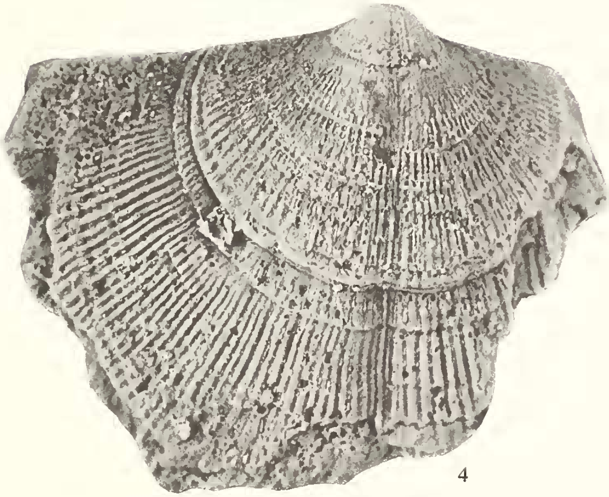

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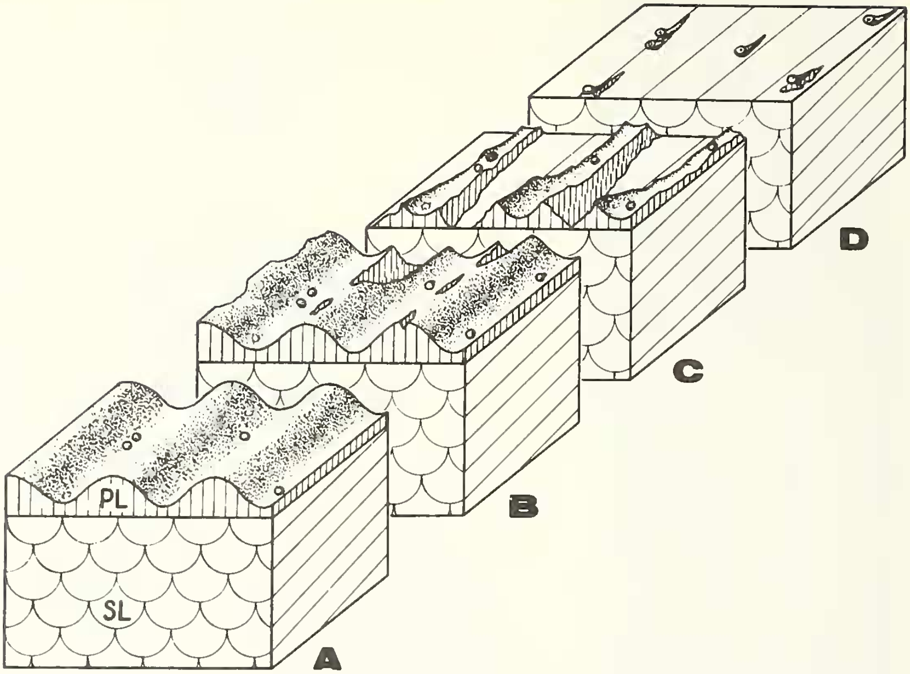


TEXT-FIG. 1. Diagram of secondary changes in micro-ornamentation of *Ilmenia hians* (Buch) (not in scale); PL—primary shell layer; SL—secondary shell layer.

from the Givetian of Moravia (Havlíček 1959, p. 182, pl. XXVII, figs. 15, 17). It is very likely that the genesis of the 'microspinosity' is identical in the two forms.

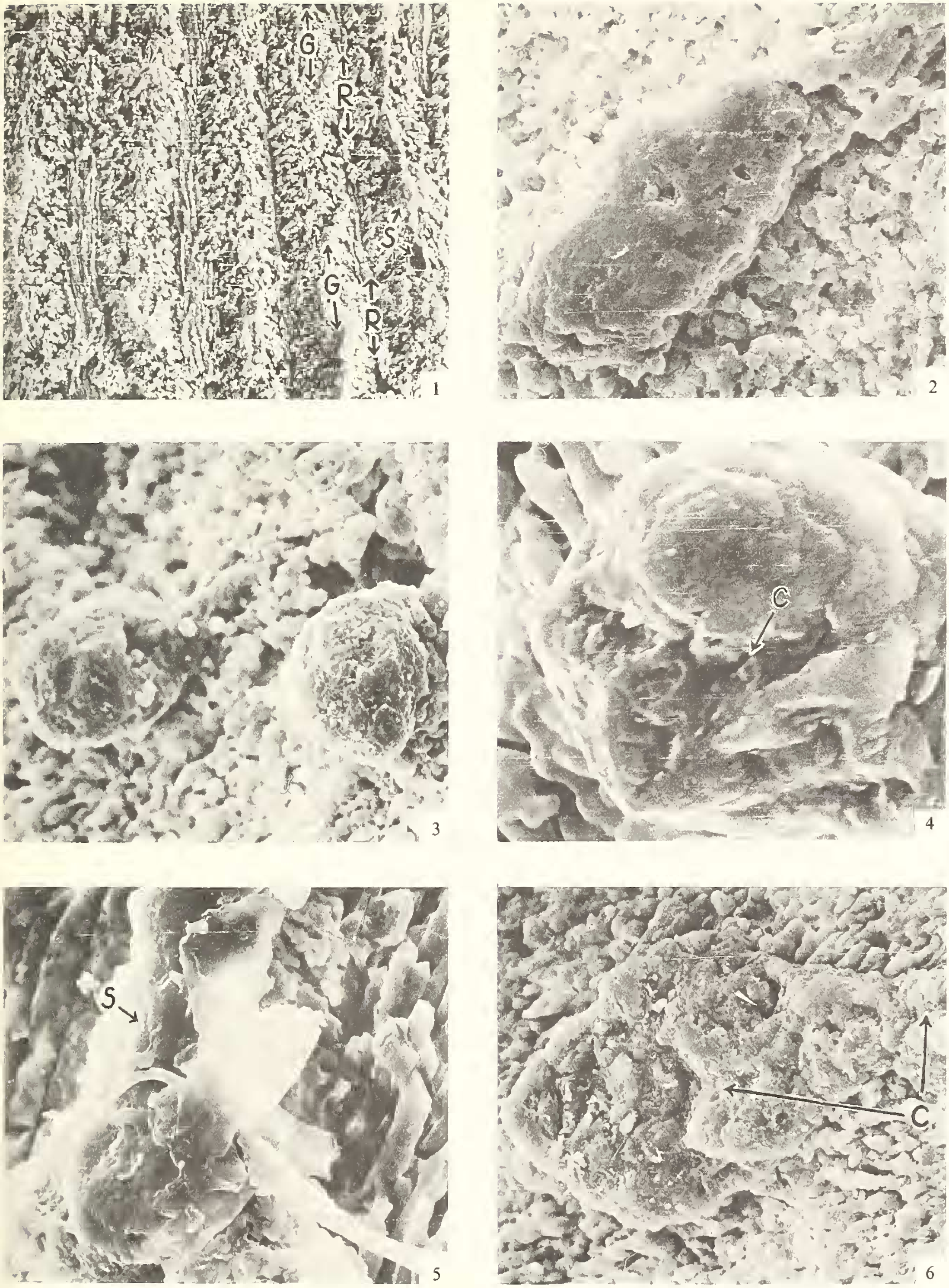
A general pattern of the distribution of 'microspines' in *I. hians* sometimes resembles a chequerboard. Commonly, however, they are fairly irregularly arranged in radial streaks between capillae, with closely spaced 'microspines' distributed along several different radial lines.

Ambothyris George and *Crurithyris* George

Most species of the genus *Crurithyris* George and a representative of a related genus, *Ambothyris infima* (Whidborne) (Baliński 1973), are marked by a presence of 'microspines', which make up an important diagnostic character, interpreted as a primary ornamental feature. The present studies indicate, however, that this type of ornamentation was developed secondarily in a similar way as in *I. hians*.

EXPLANATION OF PLATE 33

Figs. 1–6. Scanning electron micrographs. 1, an inversion of the primary micro-ornamentation on the pedicle valve of *Ilmenia hians* (Buch). Ridges, formed of the primary shell layer originally corresponding to intercapillary grooves, are visible. The secondary shell layer observed in depressions (primary-capillae), ×130. 2, 5, various morphological types of 'microspines' in *I. hians* (Buch), ×800. 3, 4, 6, various morphological types of 'microspines' in *Ambothyris infima* (Whidborne). The primary shell layer observed in all specimens; ×800, ×2400, ×800 respectively.



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In some specimens of *Crurithyris inflata* (Schnur) with a well-preserved primary shell layer, no 'microspines' are visible (Pl. 34, fig. 2 (bottom half of the micrograph)). Upon weathering a fibrous, secondary shell layer is exposed, with the simultaneous separation of initially invisible, coarsely crystalline structures embedded in the primary shell layer (Pl. 34, fig. 1).

The distribution of 'microspines' in *Ambothyris* and *Crurithyris* is not identical. In *C. inflata* a concentric distribution, conformable with growth layers, is the predominant type of distribution (Biernat 1966, p. 123, pl. XXIX, fig. 9), while in *A. infima* and *C. jurkowicensis* a radial distribution predominates, as in *I. hians*. The concentric distribution of 'microspines' in *C. inflata* was probably emphasized by an exfoliation of concentric growth layers overlapping each other.

MORPHOLOGY OF 'MICROSPINES'

In the ambocoeliids studied, the 'microspines' display a considerable differentiation resulting from the morphogenetic variability and differences in the state of preservation.

In *A. infima* (Whidborne) and *C. inflata* (Schnur) the 'microspines' are somewhat pipe-like in general outline. In their basal part they are elongate and fusiform, but anteriorly they greatly increase in size and rise (Pl. 33, figs. 3, 4, 6; Pl. 34, figs. 4, 6; Pl. 35, figs. 1–4). They are generally devoid of a distinct trace of central canal; its presumed traces only very rarely being observed (Pl. 33, figs. 4, 6; Pl. 35, fig. 2).

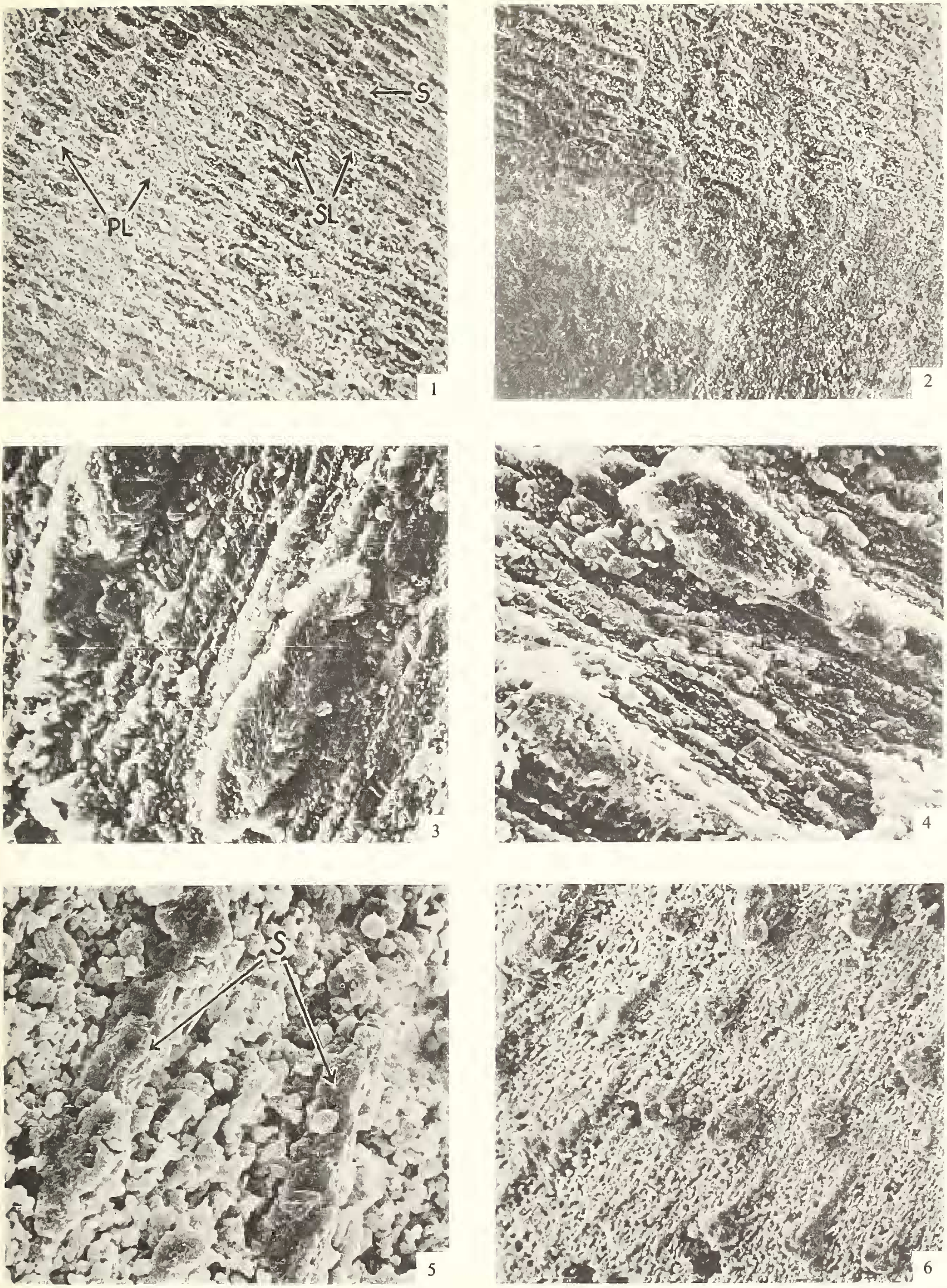
In *I. hians*, much as in *Crurithyris*, the 'microspines' consist of a prostrate basal part and an erect anterior portion (Pl. 33, fig. 5). 'Microspines' (probably strongly corroded), differing considerably morphologically from those described above, are also observed in all the ambocoeliids studied. They are elongate, fusiform, and extended anteriorly. When viewed highly magnified, they display a coarsely crystalline structure and a lack of any traces of central canal (Pl. 33, fig. 2; Pl. 34, figs. 3, 5).

DISCUSSION

In the ambocoeliids, like in other spiriferids, the 'microspines' occur only in the primary shell layer. According to many authors (George 1931; Williams 1956; Vandercammen 1959), all these elements are spines *sensu stricto*, since they had to contain the appendices of the mantle epithelium in their cavities. They might function for a relatively short time and only along the anterolateral margins of the mantle.

EXPLANATION OF PLATE 34

Figs. 1–6. Scanning electron micrographs. 1, 2, a primary (fig. 2—bottom half of the micrograph) and secondary (fig. 1—upper part of the micrograph) micro-ornamentation in *Crurithyris inflata* (Schnur), ×50. 3, 4, various morphological types of 'microspines' in *C. inflata*. Primary shell layer not preserved, only the crystals of the secondary shell layer visible, ×800. 5, 'microspines' of *C. jurkowicensis* Baliński, ×800. 6, 'microspines' of *Ambothyris infima* (Whidborne). A weathered primary shell layer visible, ×240.



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During the shell secretion, these appendices were retracted and the cavities of spines lost their contact with the shell interior (George 1931).

However, the 'microspines' of the ambocoeliids are distinctly different morphologically from analogous structures of many other representatives of the Spiriferida. In *Proreticularia dorsoplana* Gürich (Pl. 32, fig. 2) and *Nucleospira lens* (Schnur) (Pl. 32, fig. 3) they are very long, some of them reaching 0·5 mm, and bear a very distinct trace of central canal (Pl. 35, figs. 5–7). Also long tube-like spines are observed in *Reticulariina spinosa* (Norwood and Pratten) (Campbell 1959, pp. 356–358, pl. 59, figs. 10–14; pl. 60, figs. 4, 6), *Altiplectus*(?) sp. (Ivanova 1971, p. 32, text-fig. 14), and *Spiriferina* d'Orbigny (Ivanova 1971, p. 32, text-fig. 12).

The lack of unequivocal traces of the central canal in 'microspines' in the ambocoeliids studied may be explained by their filling with shell substance by the retracting appendices of mantle epithelium and by the state of preservation. In *Ambothyris infima*, however, the 'microspines' are quite distinct and some of them even display traces of a presumed central canal (Pl. 33, fig. 4; Pl. 35, figs. 2–4).

Despite the lack of unequivocal evidence, it seems that the 'microspines' in the ambocoeliids may be spines *sensu stricto* and not just structures comparable with the pustules of the terebratellacean *Kingena* Davidson (Owen 1970, pp. 41–42, pl. 13, figs. 3–5). The 'microspines' of the ambocoeliids seem to be specialized structures, homologous with true spines of other spiriferids (e.g. *N. lens* (Schnur) and *R. spinosa* (Norwood and Pratten)).

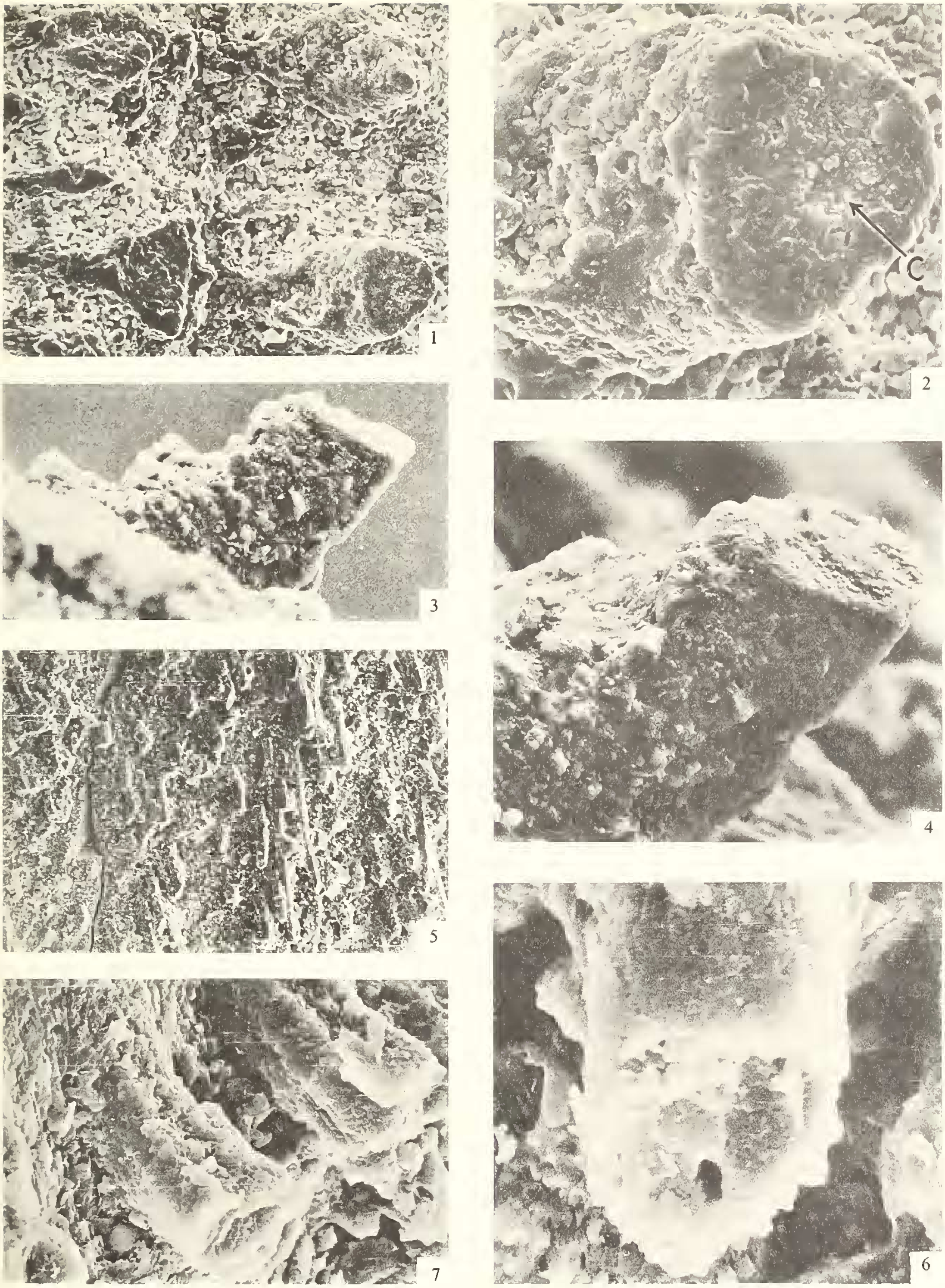
The question occurs whether the 'microspines' of the ambocoeliids were originally embedded completely in the primary shell layer or projected above its surface. The size of the 'microspines' in *Crurithyris* suggests that they did not project above this layer (Pl. 34, figs. 3–5), but in *A. infima* some of them are long, reaching 0·15 mm (Pl. 35, figs. 1–4), and it seems unlikely that the primary shell layer would have been thick enough for the 'microspines' to be completely embedded in it.

In some specimens of *I. hians* with a well-preserved primary ornamentation (capillae), distal parts of the 'microspines' are seen in intercapillary grooves (Pl. 32, figs. 1, 4), while in the remaining specimens they are invisible. This might indicate that the length of 'microspines' was subject to considerable variability within one and the same species.

Spinous elements, somewhat similar to the 'microspines' of the ambocoeliids are observed in some representatives of the Spiriferida. Such structures occur in *Phricodothyris* (Kozłowski 1914, pp. 73–74, text-fig. 18*d*), *Hysterolites*, *Paraspirifer*, *Spinocyrtia*, *Emanuella*, *Gurichiella*, and *Elytha* (see Vandercammen 1959), as well as in *Cyrtina* and *Squamularia* (see Ivanova 1962). The lack of data on the structure of microspines of these genera makes any detailed comparisons with the 'microspines'

EXPLANATION OF PLATE 35

Figs. 1–7. Scanning electron micrographs. 1, 2, 'microspines' of *Ambothyris infima* (Whidborne), ×240, ×800 respectively. 3, 4, lateral and oblique-lateral views of 'microspines' of *A. infima*; ×480, ×800 respectively. 5, 6, microspines of *Nucleospira lens* (Schnur); ×50, ×150 respectively. 7, microspines of *Proreticularia dorsoplana* Gürich, ×800.



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of the ambocoeliids on the one hand and with the microspines *sensu stricto* on the other impossible for the time being.

Despite considerable morphological differences between the spines in various spiriferids they might perform a very similar function. It is very likely that the spinosity in the Spiriferida is much more common than believed so far. Along with the advancing studies on a better-preserved material, further examples of several varieties of spinosity may be found within this group of brachiopods, but specimens are necessary with a very well-preserved primary shell layer susceptible to exfoliation.

TAXONOMIC IMPORTANCE OF MICRO-ORNAMENTATION

The examples of secondary changes in micro-ornamentation, described herein, may have important consequences to the taxonomy of this group. The occurrence of micro-ornamentation of various types in one and the same specimen, previously interpreted as a primary character, commonly taken as important at the generic level, compels investigators of the Spiriferida to be extremely cautious. The interpretation of micro-ornamentation accepted so far might cause the erection of synonymic taxa based only on the differences in micro-ornamentation, such as, for example, *Ilmenia* Nalivkin and *Ilmenispina* Havlíček. Nevertheless, it seems that both the primary and secondary micro-ornamentation might be of a considerable taxonomic importance. However, in each case, equivalent analogous elements should be compared, with the consideration of their genesis and state of preservation.

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